6—Devonian and Carboniferous Spiriferids from the North-West Basin, Western Australia *

By Brian F. Glenister †

The spiriferid fauna from the newly discovered Devonian and Carboniferous rocks of the North-West Basin of Western Australia is described. One new genus and species, *Austrospirifer variabilis*, and four new species, *Cyrtospirifer minilyaensis*, *C. australis*, *C. gneudnaensis* and *C. brevicardinis* are described from the Upper Devonian, and three new species, *Spirifer fluctuosus*, *Punctospirifer plicatosulcatus*, and *Syringothyris spissus* from the Lower Carboniferous. The relative taxonomic value of the various morphological features in tracing phylogenetic lineages within the articulate brachiopods is critically examined. Special consideration is given to those features which affect the spiriferids, and it is concluded that the Spiriferidae constitute a single phylogenetic lineage.

Introduction

Sediments of Palaeozoic age were recorded from the North-West geographic division of Western Australia as early as 1848. Little was known of these rocks until 1907, when A. Gibb Maitland carried out a geological reconnaissance of the area. Further contributions were made by F. G. Clapp, H. G. Raggatt, and C. Teichert, so that by 1947, Teichert was able to present a fairly comprehensive account of the structure and stratigraphical succession. The North-West Basin was stated to cover an area of 40,000 square miles along the coast of the Indian Ocean, between 22° and 28°S. Rocks of Permian, Jurassic, Cretaceous and Tertiary age, with a maximum thickness of 13,000 feet, were known. They were recognized as forming a half basin, open to the sea on the western side, and bordered by the pre-Cambrian crystalline complex to the east. A regional westerly dip and a thickening of the sediments to the north were recorded.

In 1949 a field party of the Commonwealth Bureau of Mineral Resources approached the eastern margin of the Basin with the object of mapping what were believed to be the basal beds of the Permian System. In the vicinity of Williambury Station, situated at about 24° S. and 110 miles inland from the coast, a thick series of Devonian and Carboniferous marine sediments was discovered. It was from these rocks that the fossil material which forms the basis of the present paper was collected.

All type material is stored with the Bureau of Mineral Resources, Geology and Geophysics, Canberra, Australia. The type numbers given in the text are those of the Bureau of Mineral Resources, and all locality numbers used refer to the Bureau of Mineral Resources' field localities.

Stratigraphy

Nannyarra Greywacke.—This is the basal Formation of the Devonian which rests on the underlying Pre-Cambrian crystalline complex. It is unfossiliferous and of variable lithology.

Gneudna Limestone.—This Formation, which lies conformably on the Nannyarra Greywacke, consists of a fairly uniform series of limestones with a thickness of 2,500 feet. Spiriferids first appear 600 feet above the base of the Formation, and are present through a thickness of 870 feet. New species of *Cyrtospirifer* (see Table I) fix the age of this fossiliferous horizon as late Frasnian. It has been shown (Crickmay 1952) that this genus is confined to the Chemung stage of the North American successions and is distinct from the younger *Cyrtiopsis* fauna of the Famennian. The presence of over 4,000 feet of sandstone between the *Cyrtospirifer* beds and the lower Mississippian Moogooree Limestone is in accordance with this age determination. The associated fauna of the Gneudna Limestone includes corals, stromatoporoids, nautiloids, *Tentaculites*, *Atrypa*, *Hypothyridina*, and *Productella*.

TABLE I

Field No.	Distribution of Species	Feet above base of Section
206		1380
200		1220
29		1200
20	*Austrospirifer varibilis*	1180
197		1170
195		1140
194		1130
193		1120
189	*Crytospirifer minilyaensis*	1100
17		1000
184	*Cyrtospirifer brevicardinis*	975
183		965
182		960
181		950
180	*Cyrtospirifer australis*	945
178	*Cyrtospirifer gneudnaensis*	935
177		920
151		600

Stratigraphical distribution of the Upper Devonian spiriferids from the Gneudna Limestone of the North-West Basin, Western Australia. Stratigraphic horizons are given with respect to the base of the Gneudna Limestone.

Munabia Sandstone.—This Formation overlies the Gneudna Limestone with conformity. It consists of fine-grained current-bedded sandstones with some conglomeratic horizons towards the top. The thickness has been estimated at 2,850 feet. No fossils have been found, but from a consideration of the age of the underlying and overlying Formations, a Famennian age for the Munabia Sandstone seems probable.

Moogooree Limestone.—This Formation overlies the Munabia Sandstone with conformity. It is a rather uniform series of limestones and dolomitic limestones with a thickness of 900 feet. Occasional fossiliferous bands are found in the upper half of the Formation. One such band contains numerous specimens described below as new species of *Syringothyris, Punctospirifer* and *Spirifer.* The band has a thickness of 5 feet, and is situated 400 feet above the base of the Formation. The fossils are generally silicified, and were freed by dissolving the matrix in hydrochloric acid. The associated fauna includes productids and a species of *Rhipidomella.*

Syringothyris is the only genus recognized which has a moderately restricted stratigraphical range. This genus has been reported from the Permian of India, Spitzbergen and Australia, but in each of these cases the identifications were made on unsatisfactorily preserved material. The undoubted range of the genus is from Conewango to Keokuk times. *Syringothyris spissus,* the Western Australian species of *Syringothyris,* is not a typical representative of the genus, but nevertheless it seems probable that the rocks from which it came are of late Devonian (Conewango) or early Mississippian (pre-Warsaw) age.

Williambury Sandstone.—This Formation rests conformably on the Moogooree Limestone, but the lithological change is sharp. Conglomerates are characteristic of the lower part, whereas the upper parts of the Formation consist of fine-grained sandstones. The thickness of the Williambury Sandstone is somewhere in the vicinity of 2,000 feet. The nature of the stratigraphic association between the Williambury Sandstone and the overlying Permian rocks is obscure, since in all observed areas they are in contact along Tertiary fault lines. Carboniferous and Permian rocks in their respective fault blocks have the same general attitude and dip, so that no large scale diastrophism can be expected between the two Periods. The basal beds of the Permian System (Lyons Group) are almost certainly of Sakmarian age. Thus although no fossils have been found in the Williambury Sandstone, it appears from the associated rocks that this Formation is of middle or upper Carboniferous age.

Terminology and Morphology

In order to avoid ambiguity and unnecessary repetition, the precise meanings applied to several frequently occurring terms are given in the following section. Brief explanations are added where new interpretations of function or nature of morphological features have been made.

Growth Stages.—In separating specimens of two closely allied species, considerable difficulty is often found in determining whether variation is interspecific or merely a function of age of the individual specimens. It is frequently impossible to decide exactly what growth stage an

individual has reached. Since such features as the general shell shape vary with age, within wide limits, this inability to determine the age of an individual presents serious difficulties to the taxonomist. In a complex series of closely allied species, such as is found in the Upper Devonian of Western Australia, confusion may easily arise as the result of grouping mature representatives of a phylogenetically primitive stock with immature representatives of a more highly evolved group.

From the preceding remarks, it may be readily seen that the recognition of morphological features which give some indication of the age of an individual are of primary importance. Such criteria do exist, and although absolute accuracy is never attained, careful consideration of all the available data may result in a reasonable estimation of the growth stage reached by a specimen, especially when the number of specimens considered is large. The following are the growth stage terms used in the present study, with indications as to their delimitation. The *nepionic growth stage* represents the period of growth of the true shell immediately succeeding the embryonic shell or protegulum, but before undoubted specific characters become evident. Practically all spiriferids are more brachythyrid in the nepionic stage than in the neanic and ephebic stages, although they may again attain an equally brachythyrid outline in the gerontic stage. Surface macro-ornamentation is not generally well developed. During the *neanic growth stage*, all the features which characterise the adult are progessively developed. Spiriferid shells are usually megathyrid in the early neanic growth stages and may have the relative length of the hinge line reduced as maturity is approached. Features of the rostral area are never obscured by the secretion of an apical callosity in the neanic growth stage. The *ephebic growth stage* is initiated when the development of all adult specific features is completed. Spiriferids are generally more inflated at maturity than in earlier growth stages, and the area of maximum shell secretion often changes from the cardinal extremities to the anterior margin. The variations in the *gerontic growth stage* may be striking and complex. Shell secretion often results in obesity and thick shells. The rostral callosity is frequently developed to the stage where it completely obscures the finer internal structures of the rostral area. Shells which were megathyrid at maturity may become subquadrate and even brachythyrid in outline. Closely spaced lamellose growth lines are sometimes developed.

Hinge Denticles.—These are the minute elevated inward crenulations in the anterior margin of the palintrope of many brachiopods (Plate 7—6, 8, 11, 13). They are confined to the pedicle valve, and articulate with shallow *denticle pits* (Plate 8—6) in the brachial valve. *Denticle grooves* (Plate 7—8) are shallow grooves on the surface of the ventral palintrope, irregularly spaced, and orientated approximately at right angles to the hinge line; they trace the ontogeny of the hinge line crenulations.

In his study of *Syringothyris*, North (1920) noticed that well-preserved specimens of this genus possessed a palintrope which was clearly divided into three triangular portions. The two lateral portions showed growth lines parallel to the hinge line and were similar in shell structure namely in the possession of punctae, to the remainder of the shell. The central portion, which was bisected by the delthyrium, was impunctate, and in addition to horizontal growth lines showed irregularly-spaced grooves at right angles to the hinge line. These grooves were continuous with a series of minute denticles along the hinge line, the denticles articulating with shallow sockets in the brachial valve. There can be little doubt that the function of the denticles was to steady the valves, especially in forms with extended hinge lines and proportionally short teeth.

In discussing the origin of the denticles, Young (1884) suggested that they were due to the presence in the hinge line of the living animal of fibres of aragonite, which, "being harder than the ordinary calcite of the shell went to the formation of the row of denticles." He concluded that the vertical grooves on the palintrope were the result of different degrees of resistance offered by calcite and aragonite to subsequent alteration, since aragonite, though harder than calcite, is more soluble than that mineral. The corresponding pits of the brachial valve were supposed to have been formed solely by the friction of the harder projecting aragonite denticles of the pedicle valve.

The structure of these denticles and corresponding pits is shown in detail by many of the specimens of *Spirifer fluctuosus*, n.sp. from the Carboniferous of the North-West Basin, Western Australia. Minute inward folds occur at irregular intervals along the anterior margin of the palintrope. These crenulations are slightly elevated and sharply pointed, forming denticles. The narrow grooves on the surface of the palintrope, directed at right angles to the hinge line, trace the path of these hinge line crenulations through the ontogeny of the specimen. Bifurcation and anastomisation of the denticle grooves is not rare.

Techniques

Most of the Devonian spiriferids described in the present work were completely freed from matrix on their external surfaces during the weathering processes which released them from the parent rock. They were however filled with matrix, so that serial sections were necessary to reveal the internal structures.

The sectioning apparatus used consists of a horizontal mounting plate supported on a rigid tripod. The height of the attachment plate above the plane of the tripod legs may be adjusted by a micrometer screw graduated in intervals of 0.01 mm. Fossils are attached to the plate with sealing wax, and parallel serial sections ground by moving the tripod on a sheet of plate glass, so that the fossil moves with a circular motion over an abrasive disc held rigidly in the centre of the glass sheet. Section intervals of 1 mm. were found satisfactory in most specimens, although it was sometimes necessary to reduce the section interval to 0.5 mm. to gain a clear indication of some of the finer structures of the rostral area.
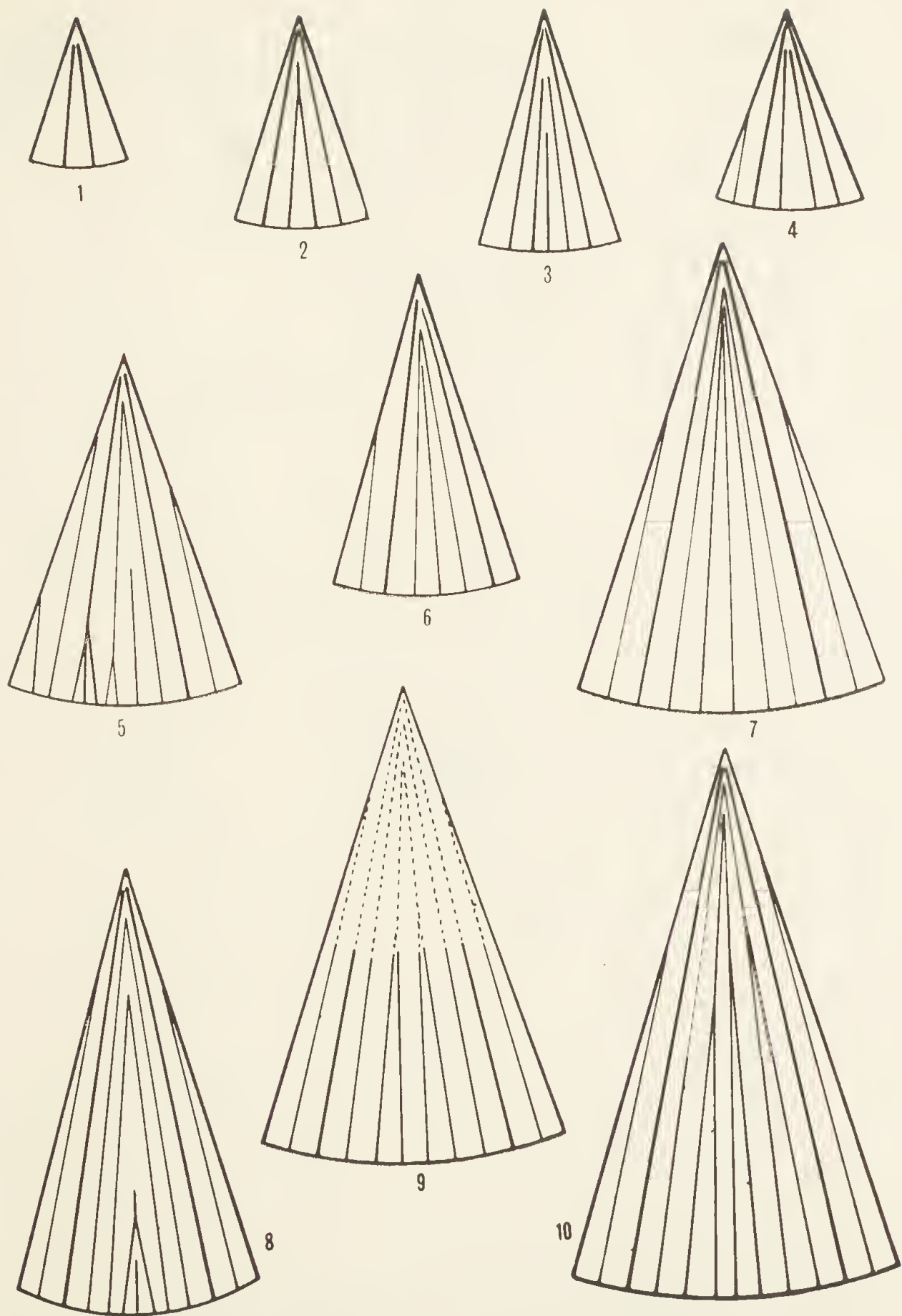
Fig. 1.—Scale diagrams of sinal plications (length x 2, width x 4).

1-4—*Austrospirifer variabilis* Glenister, n.gen., n.sp. 1, hypotype No. 449; 2, hypotype No. 450; 3, holotype No. 426; 4, hypotype No. 453.

5-10—*Cyrtospirifer gneudnaensis* Glenister, n.sp. 5, hypotype No. 466; 6, hypotype No. 467; 7, hypotype No. 468; 8, hypotype No. 469; 9, holotype No. 428; 10, hypotype No. 471.
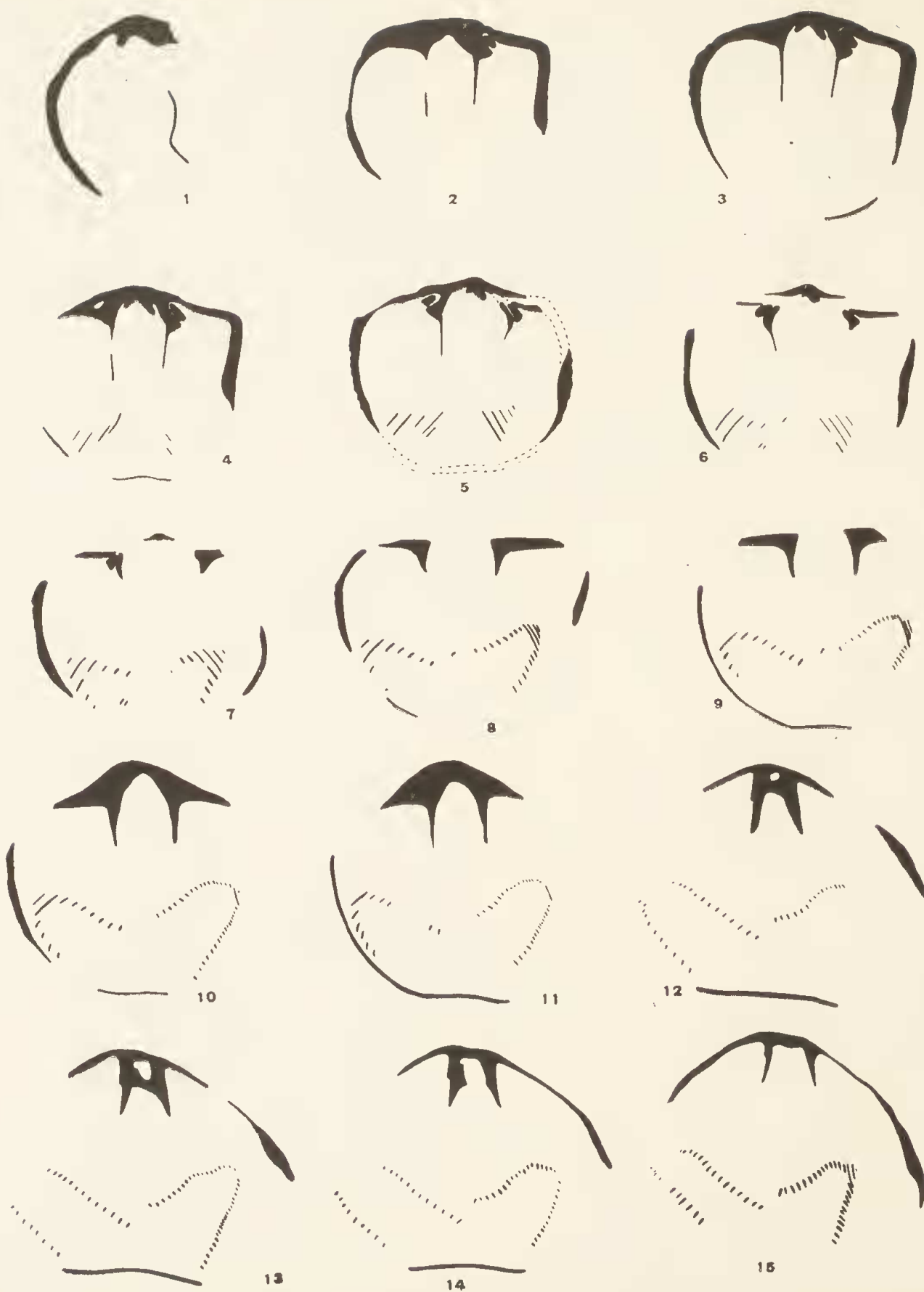
Fig. 2.—1-15—*Cyrtospirifer australis* Glenister, n.sp. Serial sections taken at 1 mm. intervals on paratype No. 440 parallel to the plane of commissure, x 1.2 (approx.). The figures were drawn onto photographic positives, made by using the celluloid serial sections as photographic negatives.
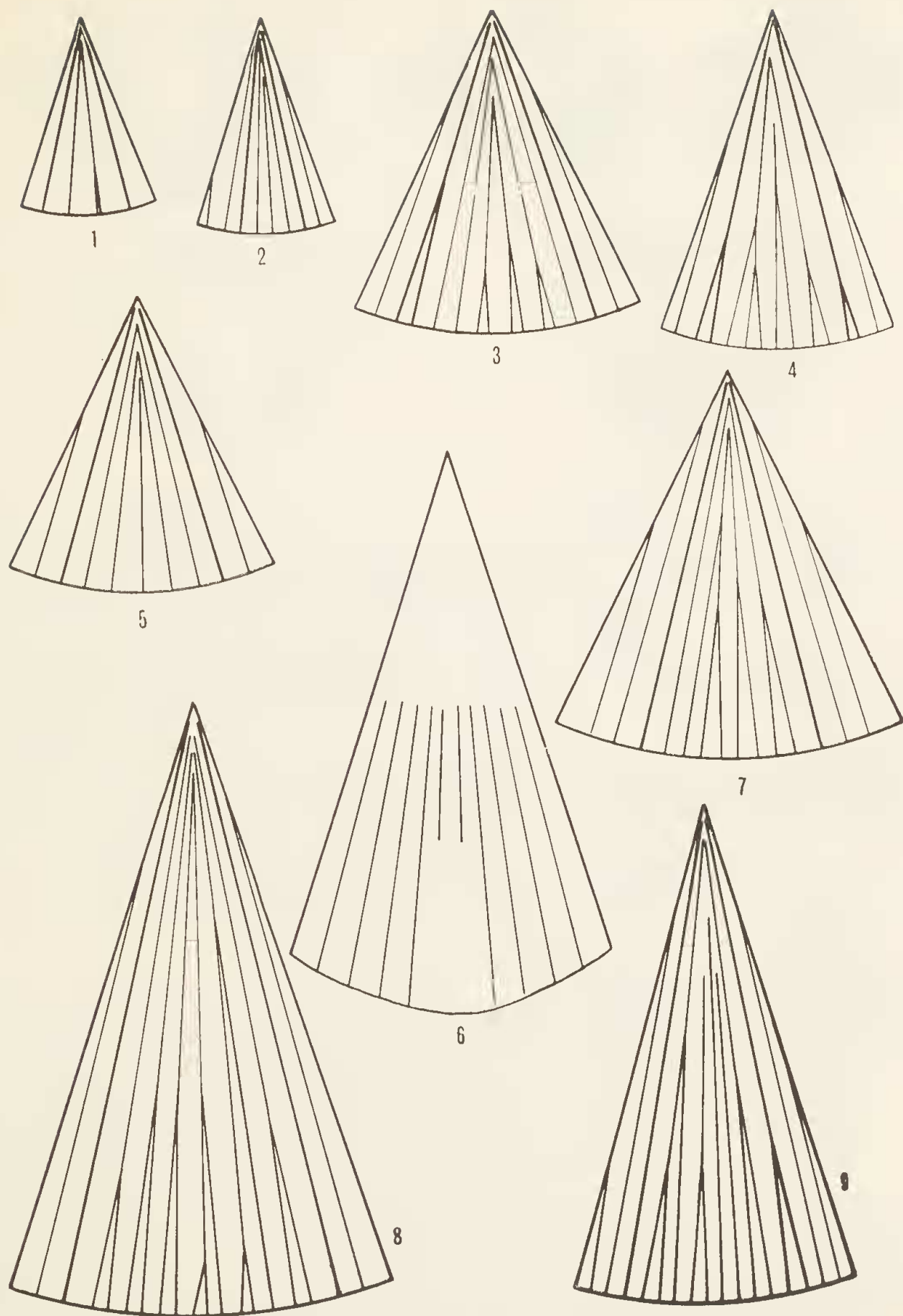
Fig. 3.—Scale diagrams of sinal plications (length x 2, width x 4).

1-5—*Cyrtospirifer minilyaensis* Glenister, n.sp. 1, hypotype No. 457; 2, hypotype No. 458; 3, hypotype No. 459; 4, hypotype No. 460; 5, holotype No. 477.

6.—*Cyrtospirifer brevicardinis* Glenister, n.sp. Holotype No. 429.

7-9—*Cyrtospirifer australis* Glenister, n.sp. 7, hypotype No. 461; 8, holotype No. 427; 9, hypotype No. 463.
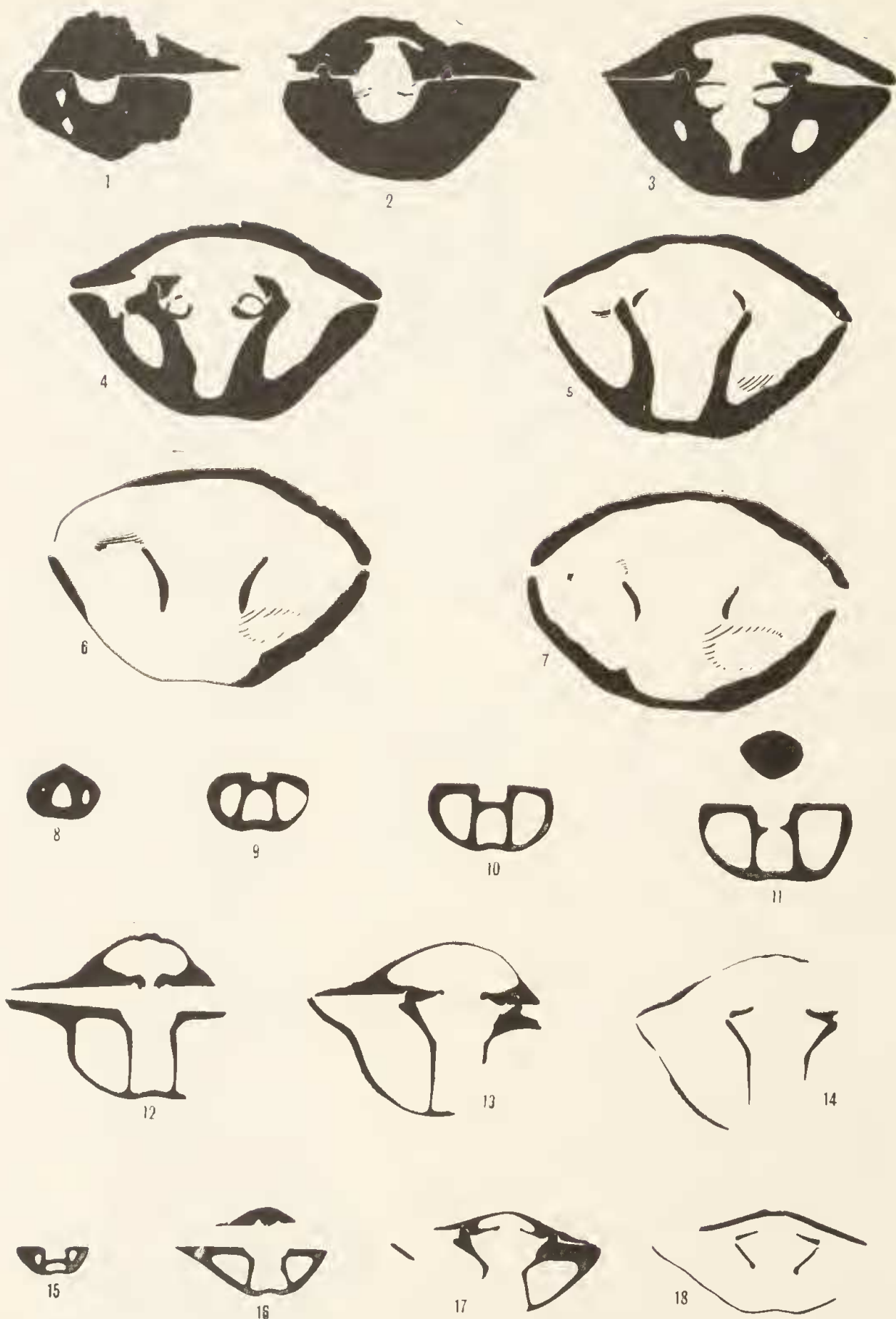
Fig. 4.—Serial sections taken at 1 mm. intervals at right angles to the plane of commissure, x 1.7 (approx.). The figures were drawn onto photographic positives, made by using the celluloid serial sections as photographic negatives.

1-14—*Cyrtospirifer australis* Glenister, n.sp. 1-7, paratype No. 441; 8-14, paratype No. 439.
15-18—*Cyrtospirifer gneudnaensis* Glenister, n.sp. Paratype No. 442.
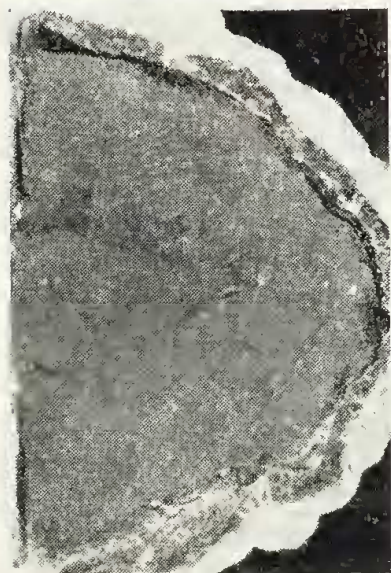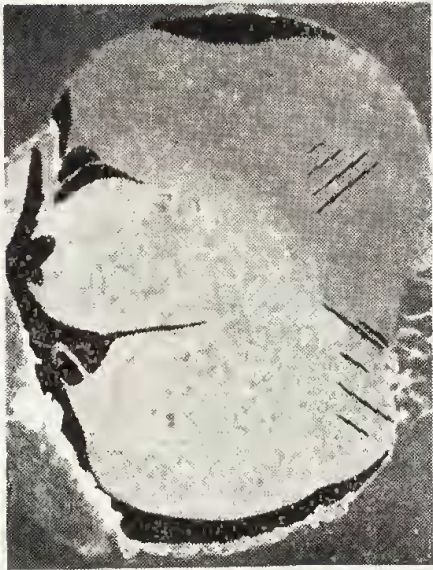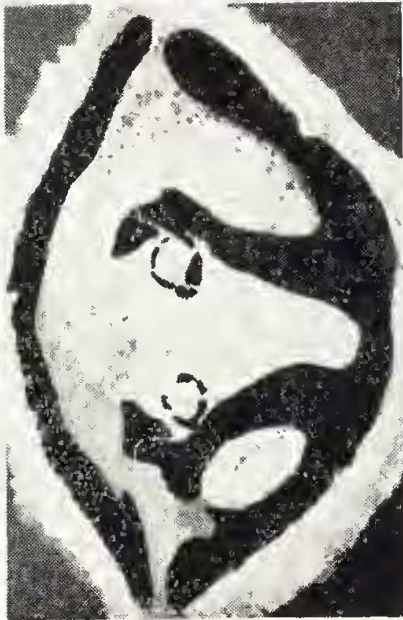
PLATE 1
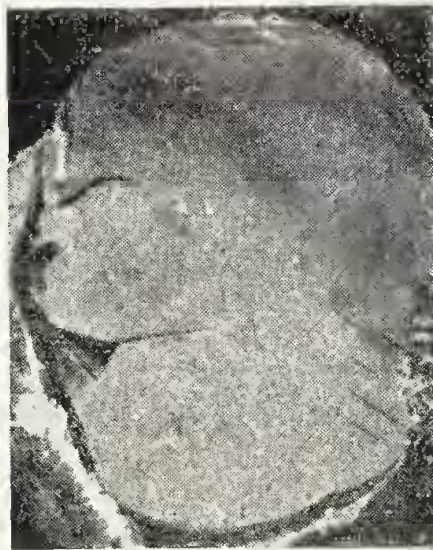
Successive stages in the construction of serial section diagrams. All figures x 2.

1-3—*Cyrtospirifer minilyaensis* Glenister, n.sp. Paratype No. 438.

4-9—*Cyrtospirifer australis* Glenister, n.sp. 4-6, paratype No. 440; 7-9 paratype No. 441.
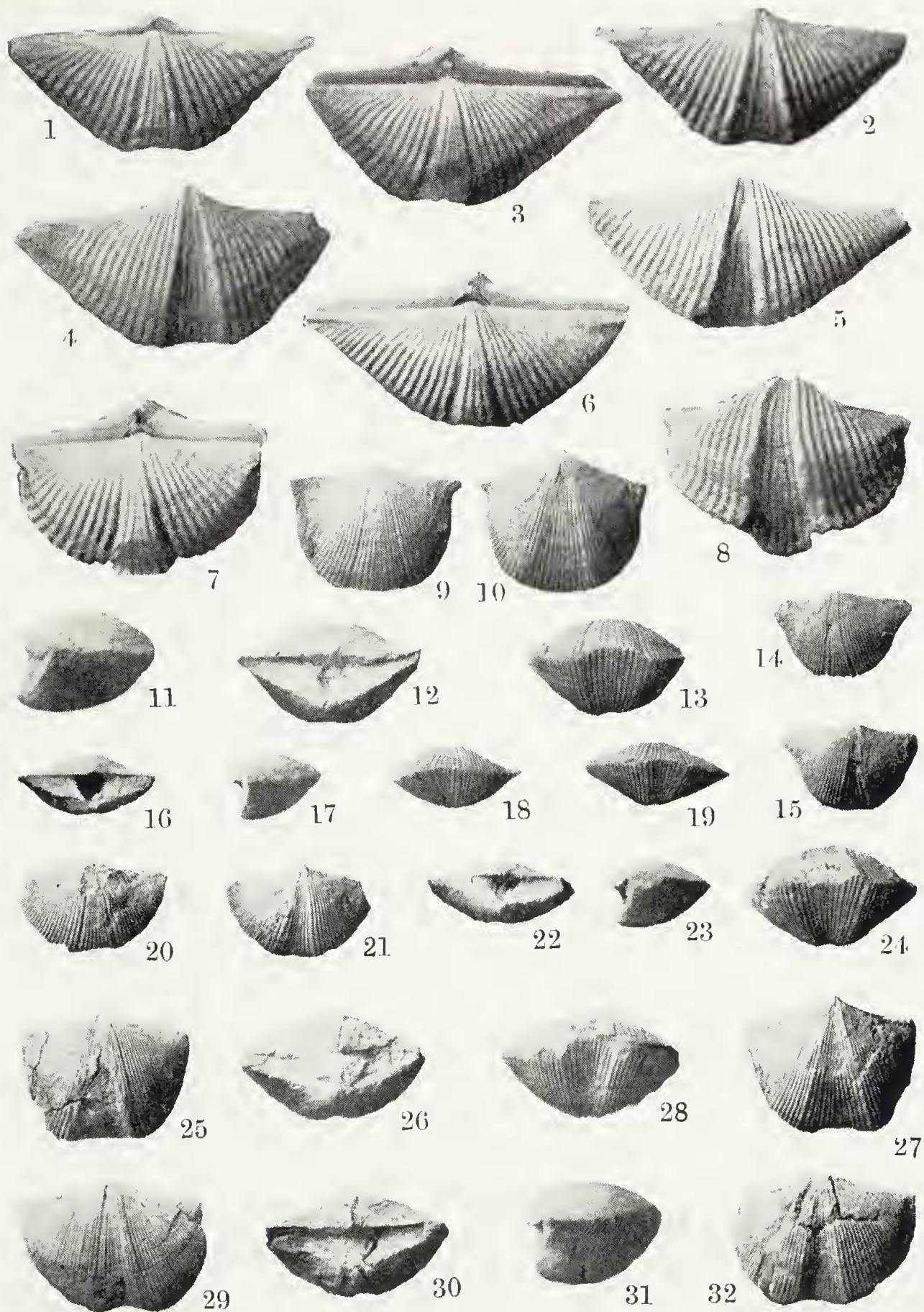
PLATE 3

1-8—*Austrospirifer variabilis* Glenister, n.gen., n.sp. All figures x 2. 1-2, hypotype No. 453; 3-4, hypotype No. 454; 5-6, hypotype No. 455; 7-8, hypotype No. 456.
9-32—*Cyrtospirifer minilyaensis* Glenister, n.sp. All figures x 1. 9-13, holotype No. 477; 14-18, hypotype No. 457; 19-23, hypotype No. 458; 24-27, hypotype No. 459; 28-32, hypotype No. 460.

PLATE 5

1-5—*Cyrtospirifer australis* Glenister, n.sp. All figures x 1. Hypotype No. 465.
6-27—*Cyrtospirifer gneudnaensis* Glenister, n.sp. All figures x 1. 6-10, holotype No. 428;
11-13, paratype No. 443; 14-18, hypotype No. 466; 19-22, hypotype No. 467; 23-27, hypotype No. 468.
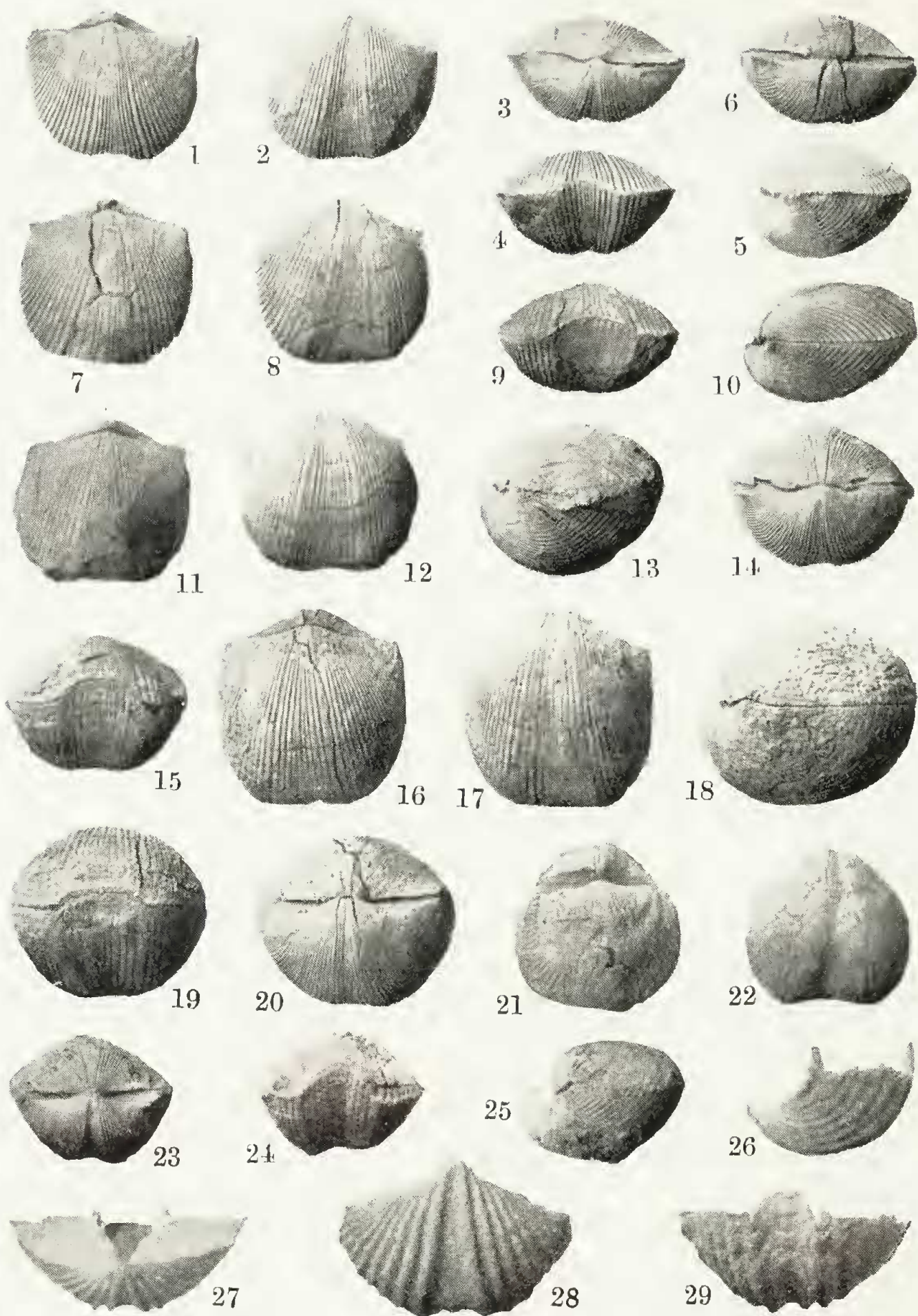
PLATE 6

1-20—*Cyrtospirifer gneudnaensis* Glenister, n.sp. All figures x 1. 1-5, hypotype No. 469; 6-10.
hypotype No. 470; 11-15. hypotype No. 471; 16-20, hypotype No. 472.

21-25—*Cyrtospirifer brevicardinis* Glenister, n.sp. All figures x 1. Holotype No. 429.

26-29—*Punctospirifer plicatosulcatus* Glenister, n.sp. All figures x 2. Holotype No. 431.
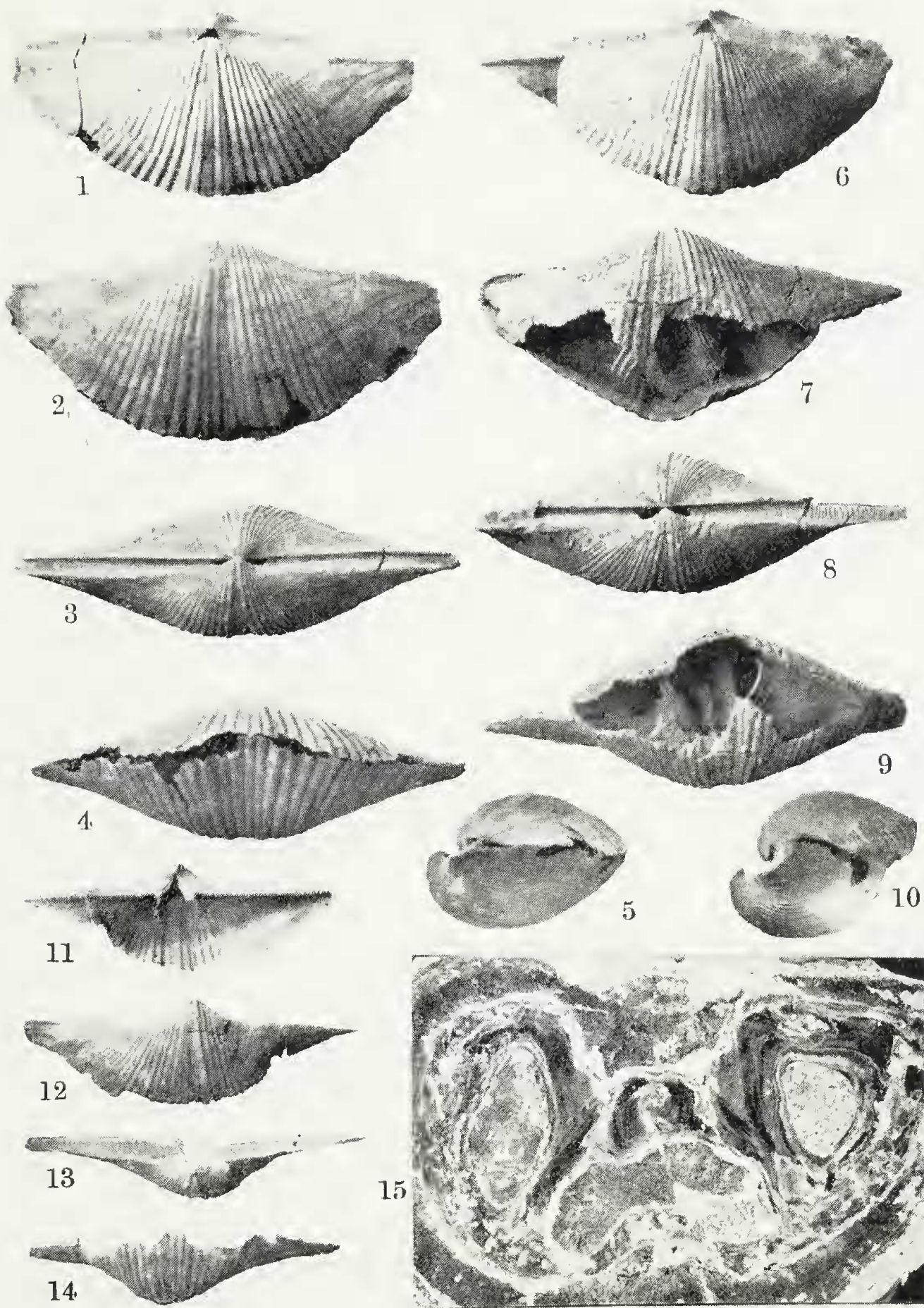
PLATE 7

1-14—*Spirifer fluctuosus* Glenister, n.sp.   All figures x 1.   1-5, holotype No. 430; 6-10, paratype
No. 479; 11-14, paratype No. 445.
15—*Syringothyris spissus* Glenister, n.sp.   Paratype No. 480, x 3.   The figure is a photographic
positive produced by using a celluloid peel as a photographic negative.
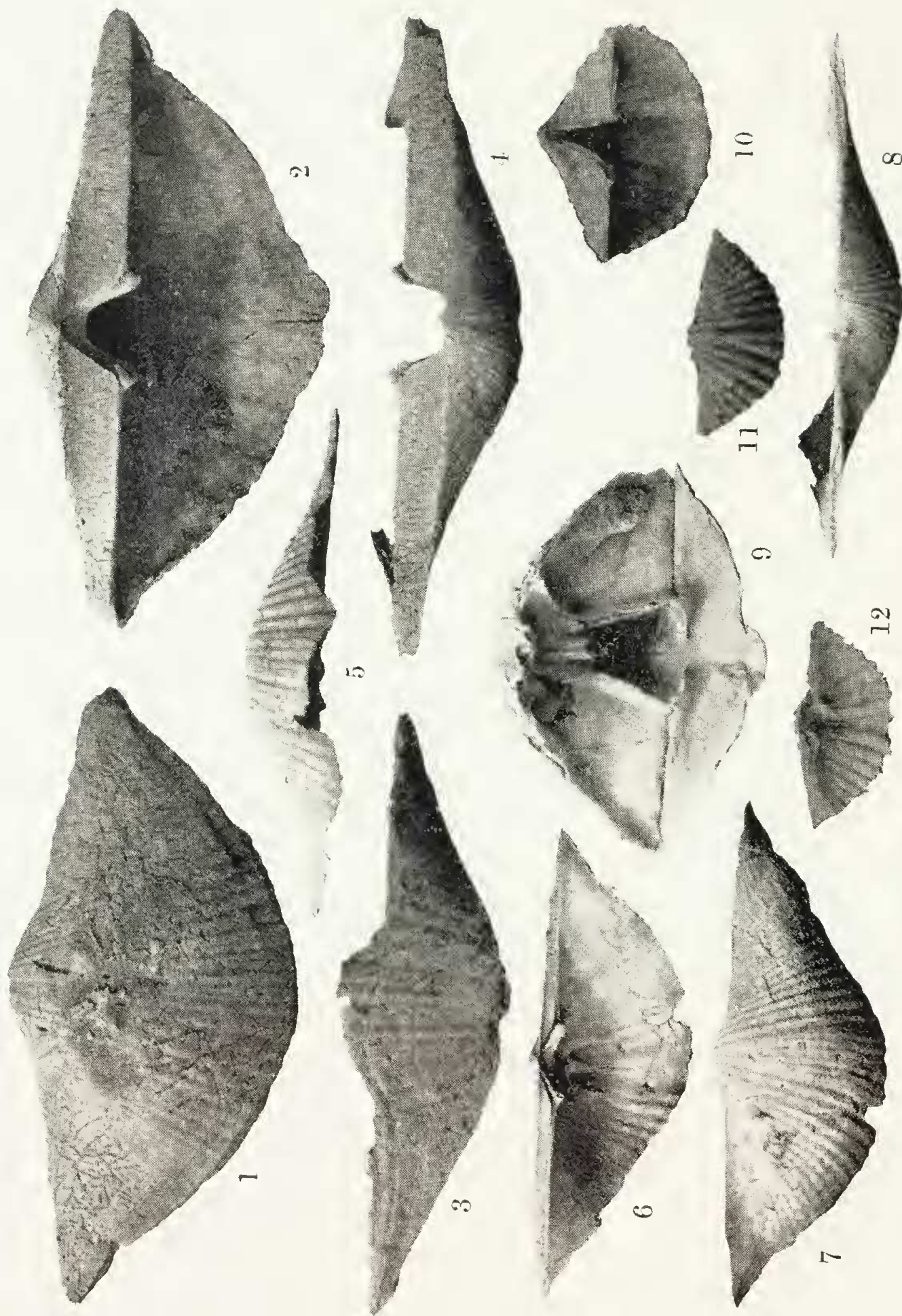
PLATE 8

1-8—*Spirifer fluctuosus* Glenister, n.sp. All figures x 1. 1-4, paratype No. 446; 5-8, paratype No. 444.
9.—*Syringothyris spissus* Glenister, n.sp. Holotype No. 432, x 1.
10-12—*Punctospirifer plicatosulcatus* Glenister, n.sp. All figures x 2. 10, holotype No. 431; 11-12, paratype No. 447.
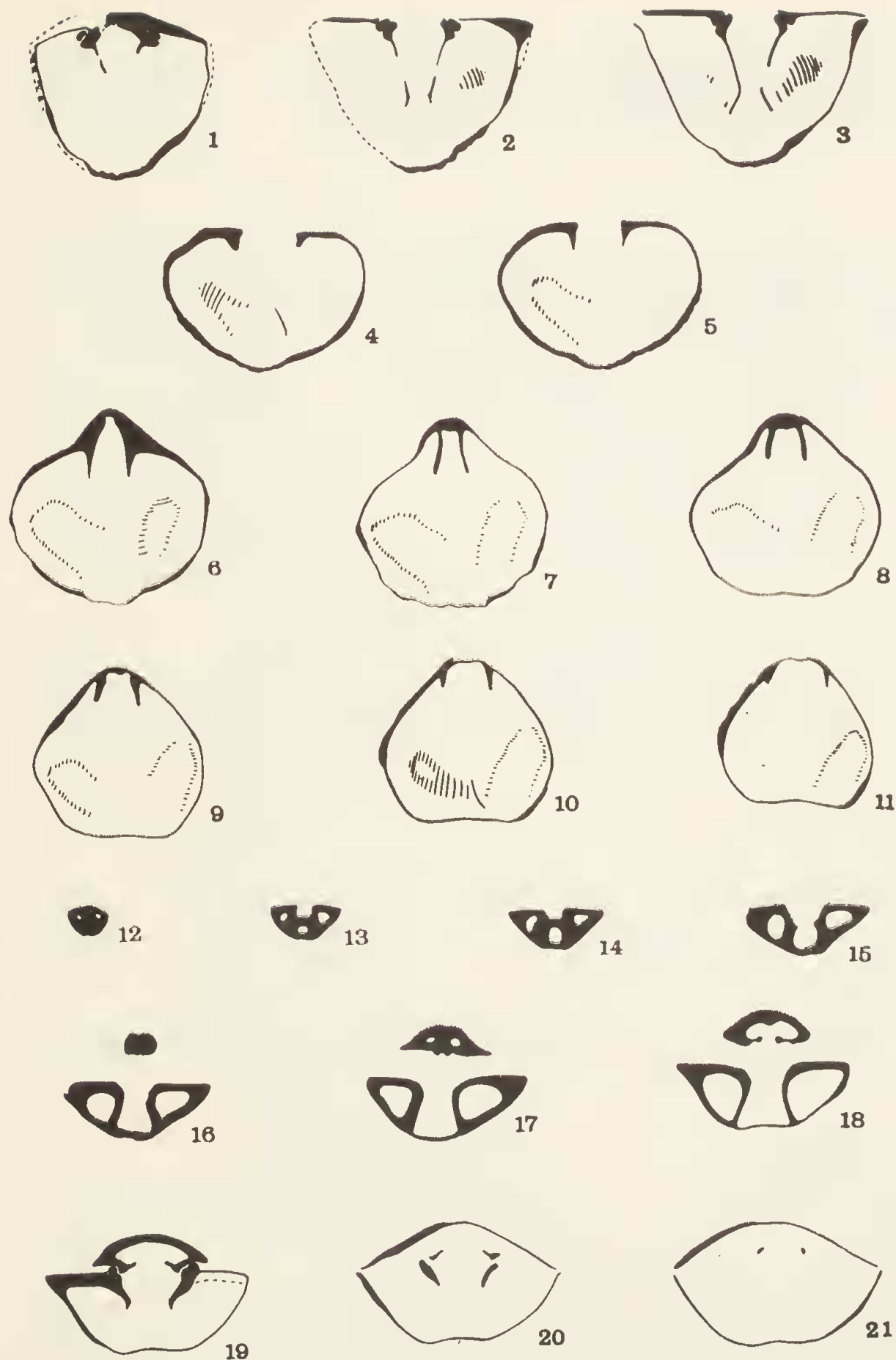
Fig. 5.—1-21—*Cyrtospirifer minilyaensis* Glenister, n.sp. Serial sections drawn onto photographic positives produced by using the celluloid pulls as photographic negatives, x 1.2 (approx.). 1-11, sections of paratype No. 438 taken parallel to the plane of commissure; 1-3 at 0.5 mm. intervals, 4-11 at 1 mm. intervals. 12-21, sections of paratype No. 437 taken at 1 mm. intervals at right angles to the plane of commissure.
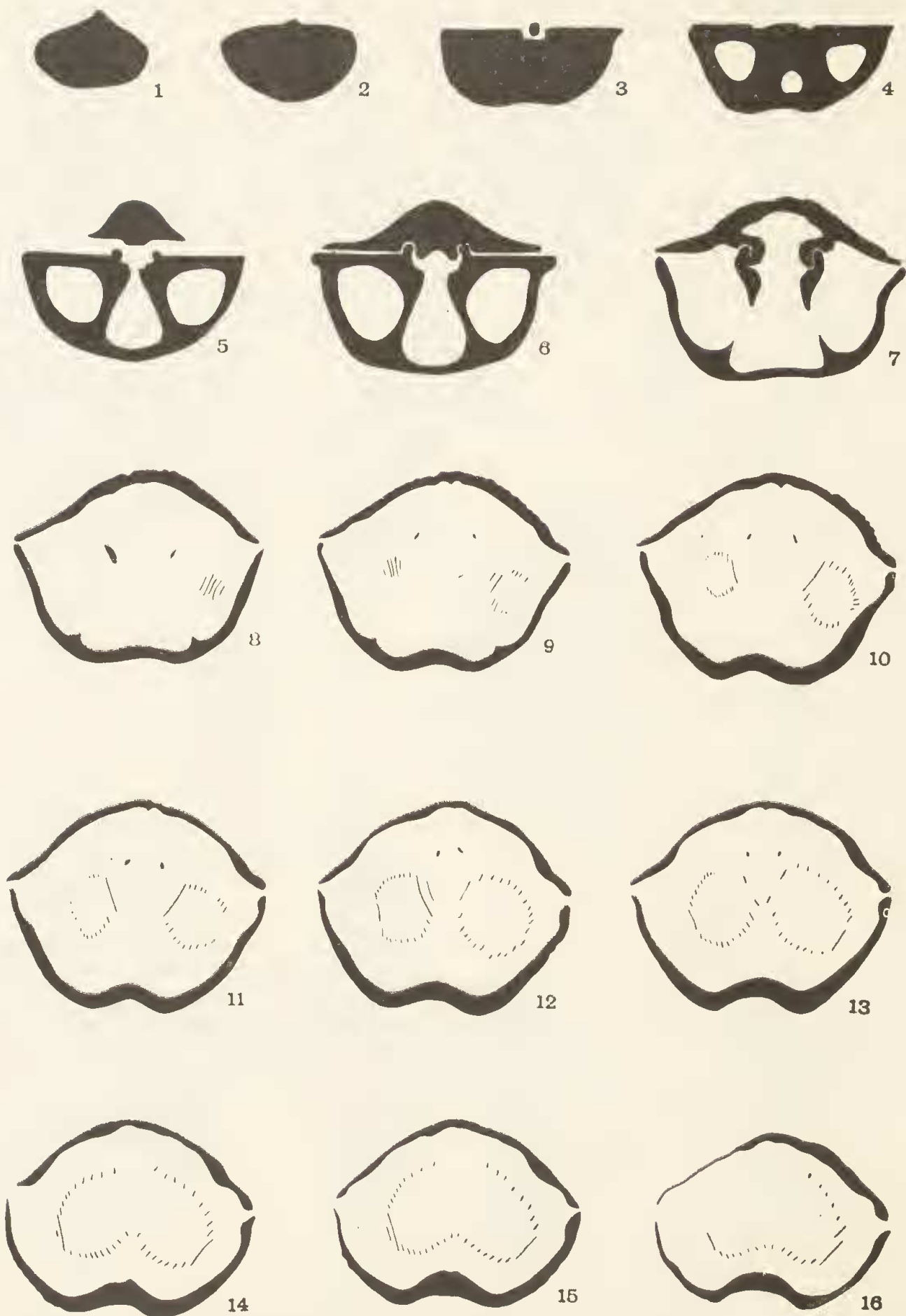
Fig. 6.—1-16—*Cyrtospirifer brevicardinis* Glenister, n.sp. Serial sections taken at 1 mm. intervals from paratype No. 478 at right angles to the plane of commissure, x 2 (approx.). The figures were drawn onto photographic positives, made by using the celluloid serial sections as photographic negatives.

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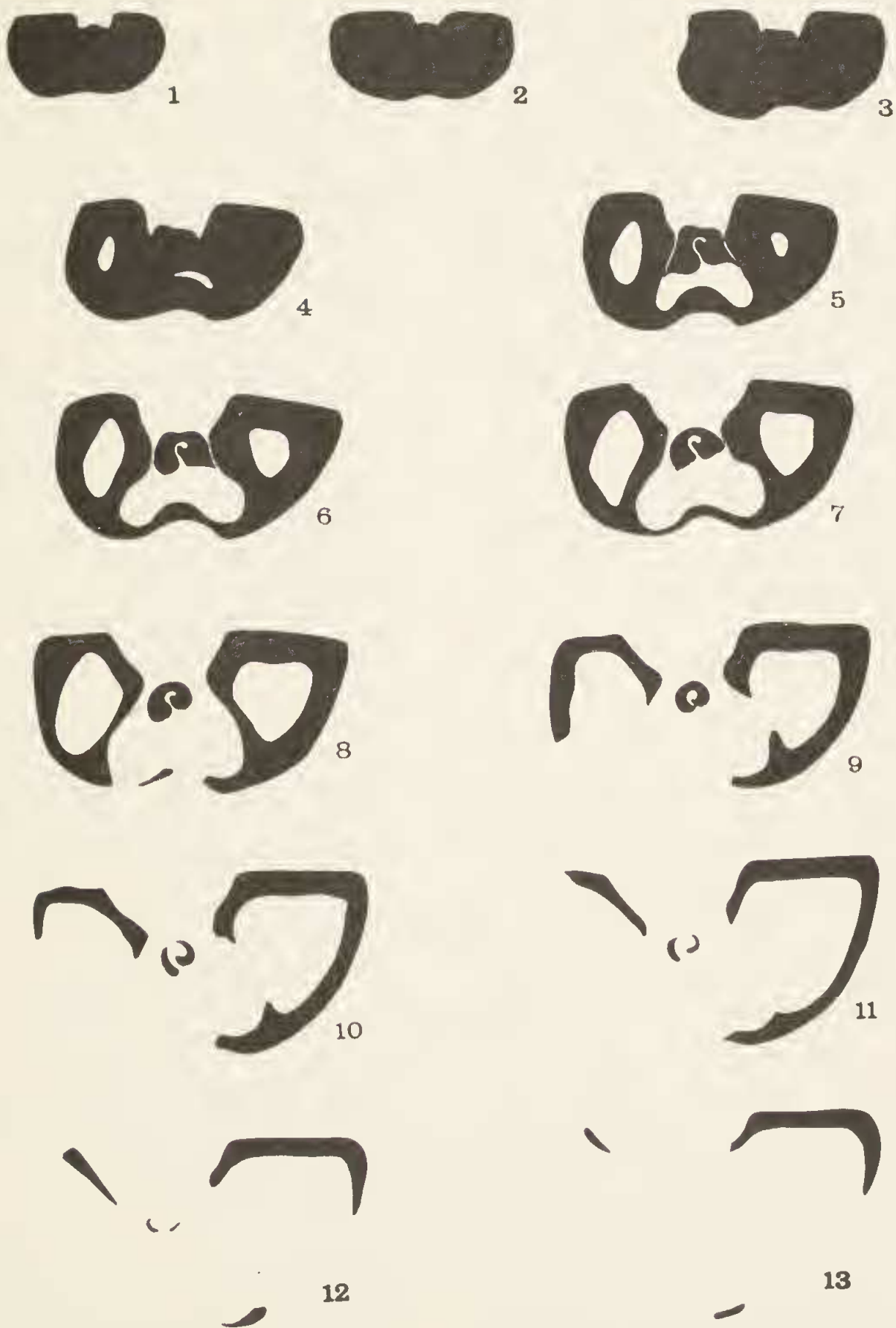
Fig. 7—1-13—*Syringothyris spissus* Glenlster, n.sp , Serial sections taken at 1 mm. intervals from paratype No. 480 at right angles to the plane of commissure, x 1.5 (approx.). The figures were drawn onto photographie positives, made by using the eelluloid serial sections as photographie negatives.

Successive planes were etched with 5 per cent. hydrochloric acid, and a celluloid peel taken at each, using the dry peel technique outlined by Sternberg and Belding (1942). A small vice with felt-lined jaws was used to clamp the moistened surface of the celluloid sheet to the etched surface of the fossil. By using considerable pressures in the vice, it was found that less solvent could be used on the celluloid sheet. Peels were thus ready for removal in three to four minutes. The celluloid used was equal in thickness to the section interval. Thus when the celluloid peels are superimposed in their correct order, they give a three dimensional model of the fossil.

Photographic positives were made, using the celluloid peels as negatives (Plate I). Ink drawings of the organic structures were then traced directly on to the photograph, and the photographic images dissolved when the ink dried. The line drawings of the serial sections were then ready for mounting.

Practically the whole fauna of the Carboniferous Moogooree Limestone has suffered at least surface silicification. Many of the brachiopods have had their shell substance completely replaced by silica in such a manner that the finest structural details are faithfully preserved. Large blocks of limestone were collected and the fossil content freed in an acid bath.

Classification of the Spiriferidae

During the last quarter of a century, four substantially new classifications of the Spiriferidae have been proposed (Frederiks, 1926; Schuchert and Le Vene, 1929; Paeckelmann, 1931; Termier and Termier, 1949). They have little in common, since each is based on different interpretations of the relative taxonomic value which can be applied to the various morphological shell features. Modern authors have as a rule accepted the classifications of either Frederiks, Schuchert and Le Vene, or Paeckelmann, and with the notable exceptions of George (1933) and Termier and Termier (1949), no serious attempt has been made to question either the utility or the phylogenetic coherency of these classifications.

The three classifications mentioned above are alike in their approach to the problem. Each is purely morphological. They differ only in the morphological features chosen as being of taxonomic value, and the consistency with which the taxonomic criteria are applied. Fredericks (1926) presented a classification which is unrivalled in simplicity, consistency of application, and artificiality. He devised a reticulum with the ordinate and abscissa represented by the type of morphic features developed in the rostral area, and the type of shell ornamentation. Known genera were placed in their appropriate pigeon-holes. By choosing such a simple network of co-ordinates, Frederiks was forced to confine his use of taxonomic features to those represented by the two co-ordinates. Groups previously defined on features other than those used by him were readjusted to fit the reticulum, thereby losing much of their original meaning. The morphological criteria which form the basis of the classification presented

by Schuchert and Le Vene (1929) are not expressly stated. An examination of this work reveals that a wide variety of morphic features is utilised. Despite the variety of features used, the classification is entirely morphogenetic and takes only scant account of the phenomenon of homeomorphy, which is so common amongst the Spiriferidae. Paeckelmann's (1931) approach was again partly morphogenetic. Punctation and jugal structures were considered to be of major taxonomic importance. The artificiality of such treatments becomes evident when the taxonomic units which result from them are compared. Corresponding subfamilies are so dissimilar that the names lose practically all meaning, and if the classifications are to be rigidly followed, the scope of many genera must be altered.

Numerous abortive attempts have shown that morphogenetic classifications are of necessity static; with difficulty they may be so constructed that they satisfactorily embrace most known facts, but they can not be made sufficiently complex to accommodate new material. The only taxonomic groups which are sufficiently flexible to include new units are purely phylogenetic. The classification of such a diverse group as the Spiriferidae cannot become stable until it is founded on a phylogenetic basis. Only then can the problem of frequent homeomorphy be overcome. An attempt in this direction has recently been made by Termier and Termier (1949). Their classification is the most satisfactory yet proposed.

Phylogeny can of course, be traced only by reference to the evolving morphological features. The problem of deciding which morphological features present traceable lines of development immediately presents itself. In deciding this question, it must be remembered that different features can not be expected to evolve at the same rate. The degree of stability of any structural feature may also vary within a group when the group is considered over a long period.

The remaining part of this section will be devoted to a consideration of the relative taxonomic value of the more important morphological features of the Spiriferidae. It must however, be remembered, that the relative stability of any morphological feature may vary between different evolving stocks. It is also necessary to again stress that the degree of morphological stability generally varies through wide limits within a particular group when that group is considered over a long period of time. Thus many of the statements made below are of necessity generalisations.

Internal Structures.—Without doubt the most stable feature of the spiriferid shell was the form of the brachidium. From the Silurian to the Triassic the spiralia remained sufficiently constant in form to defy any attempt to split the family on this feature. In some genera the spiralia of the brachidium remained separated, but in more advanced genera they were joined by the ultimate fusion of the jugal processes. The stage of development of the jugal processes is often difficult to determine, but this feature seems to be of considerable taxonomic value.

Dental lamellae developed independently in many spiriferid groups, but they nevertheless form a valuable criterion for tracing evolutionary lines. Many genera may be clearly defined by reference to some modification of the dental lamellae. Thus *Cystina* possesses strong dental lamellae which fuse ventrally to form a spondylium, *Cyrtospirifer* has its well-developed subdelthyrial platform, and *Spirifer* s.s. is characterised by short thick dental lamellae which are confined to the rostral area of the shell. An interesting modification of the dental lamellae is seen in *Syringothyris*. Here the inner layer forms a subdelthyrial platform as in *Cyrtospirifer*. However, in the plane of symmetry where the two components of the subdelthyrial platform meet, the distal edge of each component is rolled to form an anteriorly projecting closed tube, the syrinx. (Plate 15—8; plate 8—9; fig. 6.). The inner surface of the syrinx is composed of radially arranged lamellae, suggesting that this structure served as an area of muscle attachment. Median septa are frequently developed in both valves, but they are of limited taxonomic value, since they tend to be obliterated in the late ephebic growth stage by the development of rostral callosities. The nature of the socket plates is often difficult to detect, but is doubtless of taxonomic value. The diverse types of socket plates are illustrated by *Cyrtospirifer*, *Spirifer* s.s. and *Austrospirifer*. The socket plates of *Cyrtospirifer* are not directly supported by lamellae beneath them, while those of *Austrospirifer* and *Spirifer* are supported to the extent that the sockets appear as pits in the posterior shell wall. *Spirifer* has long narrow sockets, while the sockets of *Austrospirifer* are uniformly hemispherical. The development of an apical callosity is of limited value in defining some genera, but is useless in tracing phylogeny. Many genera never develop thickened shells, and those which do, rarely exhibit rapid shell secretion in the rostral area until the late ephebic and gerontic growth stages.

General Form.—The general shell shape of the spiriferids is a feature which is particularly susceptible to homeomorphy. A study of the growth lines also shows that the shell index (the ratio of width along the hinge line to the length of the valve, measured in the plane of symmetry along the shell surface) varies within wide limits during ontogeny. From these facts it becomes obvious that the shell outline attained by an individual at the time of death is of little taxonomic value. However, a study of closely related species often reveals that the ontogenies of the shell outlines are similar, and that the outlines attained at maturity are dissimilar due only to a relative retardation in development of certain species. In the four species of *Cyrtospirifer* described below, the growth lines around the umbo show that the shells were brachythyrid in the nepionic growth stage. Neanic shells were megathyrid, with alate cardinal extremities. The ephebic and gerontic growth stages are marked by vigorous growth around the anterior and anterio-lateral margins and a virtual cessation of growth along the hinge line. Mature specimens thus lose their alate neanic outline and become either subquadrate or even brachythyrid. This comparison of shell outlines throughout ontogeny has proved to be of greater value than merely comparing them at some arbitrarily chosen growth stage such as at the time of death.

High cardinal areas have developed in many different spiriferid groups. Moreover, the height of the cardinal area may vary between species which are otherwise closely related. Grabau's closely knit group of *"Sinospirifer" sinensis* contains forms which show an almost continuous range from the high cardinal area of *Tenticospirifer tenticulum* to the extremely narrow cardinal area of *Sinospirifer sinensis* (mut. *alpha*). It would seem then that the degree to which the cardinal area is developed is of limited taxonomic value.

Ornamentation.—The types of ornamentation developed by the spiriferid stock are extremely diverse. Most genera can be clearly differentiated by their macro-ornamentation, and although evolutionary trends are not fully understood and homeomorphy is certainly common, this criterion seems to be of taxonomic value. The plications of the fold and sinus have been singled out for special attention by several authors, including Grabau (1931) and Gatinaud (1949, a-d). In consideration of the detailed methods used by Grabau and Gatinaud, the present author has come to the conclusion that although the ornamentation of the sinus is of considerable taxonomic value, it does not warrant the detailed treatment given by these two authors. Grabau's method was qualitative. He differentiated new species and genera using fine details of plication arrangement as the most important, and indeed in some cases the only taxonomic criterion. The artificiality of these divisions is evident when it is noted that the arrangement of plications may differ widely from one side of the sinus to the other. Depending largely on previously published figures and plates, Gatinaud carried the splitting of the plicate spiriferids to a new extreme level. His work was quantitative, some of his new formulae containing as many as 35 individual factors. Some of the factors are entirely dependent on the growth stage reached by the specimens. Since the growth stage can not be accurately determined, the formulae merely succeed in splitting material into numerous artificial units in which the variability due to the ontogenetic stage reached and true interspecific variation are confused.

Orton (1914) and Termier and Termier (1949) have suggested that the presence or absence of a fold and sinus bears a relation to the intensity of respiratory exchanges, and is thus of considerable taxonomic value. Fossil groups at least do not contradict this belief, although evolutionary trends in the development of the sinus are difficult to determine. The point of origin of the sinus is of value in separating genera. Thus *Cyrtospirifer* and *Theodossia* are almost identical except that in the former the sinus originates at the beak, whereas it originates at about the mid-length of *Theodossia*. The presence of papilose, granulose and spinose ornamentation is valuable in generic definitions, although subject to frequent homeomorphy.

Punctation.—The attention of brachiopod workers has recently been focussed on the fine details of shell structure, since Cooper (1944) proposed a classification of the Articulata based largely on the presence or absence of punctation. The division of the Articulata into Palaeotremata, Protremata and Telotremata was replaced by a grouping into Palaeotremata, impunctate Articulata, pseudopunctate Articulata, and punctate Articulata. Cooper's classification results in the splitting of the Spiriferidae of King. The impunctate spiriferids are included in the Spiriferacea (emend Cooper) and the punctate spiriferids in a new superfamily, the Punctospiracea. If this classification has any phylogenetic basis, it implies the development of a truly remarkable series of homeomorphs. The present author finds it difficult to believe that an exceedingly complex structure such as the spiriferid brachidium could develop independently in two distantly related phylogenetic lineages; namely from both punctate and impunctate stocks. It seems more reasonable to assume that the presence or absence of punctation is only of secondary phylogenetic importance. The latter assumption is strengthened by the occurrence of both punctate and impunctate forms within two other groups which in all other morphological features appear to constitute natural phylogenetic divisions. These are the Orthida, which contain the punctate Dalmanellacea, and the Rhynchonellida, which include the punctate Rhynchoporacea. The existence of the punctate Terebratulida is also significant. To assume that the punctate brachiopod groups developed from a single common stock and that the closely similar impunctate groups are a series of homeomorphs which developed from an independent stock is unreasonable.

The Western Australian material provides evidence which has an important bearing in the discussion of phylogenetic significance of punctation. A new species described below as *Syringothyris spissus* is a typical species of *Syringothyris*, except for the impunctate nature of the shell substance. The syrinx is well developed, and appears to be identical in structure with the same morphological feature of other species of *Syringothyris*. The present author is unable to believe that forms bearing such complex structures as a syrinx and laterally directed spiralia could develop simultaneously in two distantly related phylogenetic lineages. It must then be concluded that the presence or absence of punctation can not be regarded as of major taxonomic significance.

Closure of the Delthyrium.—In Beecher's classification, the method of closure of the delthyrium was the main feature by which the Articulata were divided into the Protremata and Telotremata. The delthyrium of the Protremata was supposedly restricted by the secretion of a single plate, the pseudodeltidium, which was at first situated posterior to the pedicle. Beecher considered that in the Telotremata the delthyrium was partially closed by the secretion of a pair of deltidial plates, one on either side of the delthyrium. The discovery of deltidial plates among the Protremata (Termier and Termier, 1949) and the presence of a pseudodeltidium in many spiriferids, has made obvious the artificiality of this division into Protremata and Telotremata.

The delthyrial closing apparatus of the Spiriferidae is quite unsatisfactory in the determination of phylogenies. In a great many specimens the plate or plates are unknown. They were probably dislodged soon after death, and dispersed before the enclosure of the shell in the sediment. Most species in which the plates are definitely known exhibited a protrematous type of delthyrial closure, but some species are known to develop deltidial plates. Termier and Termier (1949) have reported deltidial plates in *Spinocyrtia,* and many specimens of *Neospirifer* in the author's collections clearly show typical deltidial plates. It is thus apparent that at our present state of knowledge of the plates which restrict the delthyrium, these structures are of little value in the taxonomy of the Spiriferidae.

To sum up, the Spiriferidae is considered to be a monophyletic group characterised by the form of the brachidium. It has been subjected to frequent homeomorphy, so that no single morphological feature can be used to completely trace the lines of descent. It is suggested that lines of descent can only be traced with reference to all available morphological and stratigraphical data. Only then can the homeomorphs be separated, and small groups of closely related genera linked in natural lineages.

Systematic Descriptions

Devonian

Family **Spiriferidae** King, 1846

Subfamily **Spiriferinae** Schuchert, 1913

Genus *Austrospirifer* Glenister, n. gen.

Type Species.—*Austrospirifer variabilis* Glenister, n. sp.

Description.—This genus is proposed for small, sub-equally biconvex, completely costate, impunctuate spiriferoids with uniplicate anterior commissure. The hinge is always the widest part of the shell. The width is generally much greater than the length, but the shell ratio may approach unity in very young or gerontic specimens.

The palintrope of the pedicle valve is narrow, orthocline to gently apsacline, and narrows only slightly towards the cardinal extremities. The broadly triangular delthyrium is almost completely closed by an imperforate convex pseudodeltidium. Dental lamellae are thick and attached to the posterior wall of the shell with little or no development along the floor of the valve. A median septum traverses the posterior part of the muscle scar on the pedicle valve.

The brachial valve bears a narrow, anacline palintrope. Socket plates are thick and supported along their whole length. They enclose hemispherical sockets. The descending lamellae are straight and converge slowly to the points where they are attached to the posterior-

laterally directed, uniformly conical spiralia. Jugal processes are not developed. A low median septum traverses the posterior half of the floor of the brachial valve.

Affinities.—*Austrospirifer* is closely related to a number of Upper Devonian spiriferids, some of which have ranges extending into the Middle Devonian. *Cyrtospirifer* is distinct because of its strong dental lamellae extending along the floor of the valve, and the absence of supporting lamellae under the sockets. *Mucrospirifer* has either an unmodified fold and sinus, or a single costa in the sulcus, while *Acrospirifer* has a non-plicate fold and sinus. *Spirifer sensu stricto* is distinct in having long but narrow sockets, and in the devolopment of jugal processes.

Austrospirifer variabilis Glenister, n. sp.

Plate 2—1-18; Plate 3—1-8; Fig. 1—1-4; Tables II and III.

Description.—The holotype, 4 paratypes and 200 specimens belonging to this species, were available to the author. The two valves are subequally biconvex. Growth lines show that the shell was subquadrate and only slightly wider than long in the immediately post-embryonic stage. The early neanic stage of growth was marked by extreme development along the hinge line, so that the width often measured more than three times the length of the conch. The cardinal extremities were so delicate that they are seldom preserved complete. The ephebic stage is indicated by a retardation of development along the hinge line, and a marked increase in the length and convexity of the valves. Practically no increase in the width of the hinge line takes place in the gerontic stage, but growth continues along the anterior and anterior-lateral margins, so that some specimens have shell indices closely approaching unity. The anterior commissure is strongly uniplicate.

TABLE II

Measurements (in mm.) of Austrospirifer variabilis *Glenister, n.gen., n.sp.*

Growth stage	Neanic		Ephebic				Gerontic		
Catalogue Number †	449	450	426 *	451	452	453	454	455	456
Plates	2—11-12	2—13-14	2—1-4	2—15-16	2—17-18	..	....	....	..
Figures	1—1	1—2	1—3		....	1—4	..	....	....
Height of pedicle valve	9·0	13·1	13·0	12·3	9·8	10·7	12·4	11·9	12·5
Length on curvature (centre)	10·8	15·5	17·6	14·8	13·1	14·6	17·3	16·5	19·5
Height of brachial valve	8·0	10·6	10·5	9·0	8·4	9·5	9·9	9·7	10·2
Length on curvature (centre)	9·1	12·1	12·3	11·0	9·8	11·2	11·3	11·7	13·8
Width along hinge line	26·4	33·8	36·2	30·4	26·6	25·4	28·4	26·6	20·0
Maximum height of palintrope	2·4	2·7	2·4	2·2	1·6	1·6	2·4	2·1	2·5
Thickness of shell	5·4	6·5	8·3	6·5	6·5	7·6	8·4	8·0	9·5
Maximum width of sinus (anterior)	3·7	5·2	5·6	4·8	4·5	5·9	5·3	4·9	6·1
Number of lateral plications	13	23	20	16	14	11	15	17	13
Shell index of pedicle valve	2·44	2·18	2·06	2·05	2·03	1·74	1·64	1·61	1·02
Shell index of brachial valve	2·90	2·79	2·94	2·76	2·71	2·27	2·51	2·27	1·45

* Holotype. † These, and succeeding catalogue numbers, refer to the type catalogue of the Bureau of Mineral Resources.

TABLE III

Shell indices for the pedicle valve of Austrospirifer variabilis *Glenister, n.gen., n.sp. Measurements measured on growth lines in mm.*

Catalogue number	450							454				
Growth stage	Nep.		Nea.					Nep.	Nea.		Eph.	Ger.
Length on curvature (centre)	2·3	3·3	8·2	11·6	12·7	14·8	15·5	4·3	9·0	11·5	13·3	17·3
Corresponding width along hinge line	4·1	6·4	26·2	32·8	33·4	33·6	33·8	7·0	21·8	28·0	28·2	28·4
Shell index	1·78	1·94	3·20	2·83	2·47	2·27	2·18	1·63	3·11	2·43	2·12	1·64

A well-defined deep sinus extends along the pedicle valve from the beak to the anterior margin. The sides of the sinus are steep and the floor is narrowly rounded. At the anterior margin the sinus is produced into an angular extension which truncates the fold of the brachial valve. The umbo is not prominent and is only slightly recurved. The palintrope is narrow, tapering in width only slightly towards the cardinal extremities. It is flat or weakly

concave and ranges in aspect from orthocline to gently apsacline. Growth lines running parallel to the hinge line are occasionally preserved. A flatly triangular delthyrium bisects the palintrope. It is partially closed by a convex imperforate pseudodeltidium. The pseudodeltidium never completely closes the delthyrium, since a triangular fissure is invariably present in the base of the delthyrium.

The umbo of the brachial valve is weakly developed. At the posterior margin of the brachial valve the fold is not prominent, but towards the anterior margin, especially in mature specimens, it is strongly elevated, having almost vertical sides and a gently convex crest. The palintrope is narrow and anacline in all growth stages.

Internally the pedicle valve bears two thick dental lamellae which support the teeth. They are attached to the posterior margin of the valve, and extend along the floor for a short distance as low ridges. The dental lamellae converge to form a poorly developed subdelthyrial platform just below their mid-height. A shallow rostral cavity appears on the lateral side of each dental lamella, as well as beneath the delthyrial platform. Accelerated secretion of shell material in the gerontic growth stage tends to obscure these features. The muscle scars lie in a deep pit situated in the posterior half of the valve. The posterior part of this pit is traversed by a median septum.

The socket plates are thick, and attached to the floor of the brachial valve for their whole length. They enclose a pair of large hemispherical sockets. The descending lamellae are straight and converge slowly to the points where they are attached to uniformly conical, posterior-laterally directed spires without being supported by a jugum. The area of muscle attachment is confined to a pit in the posterior half of the shell. It is bounded by a pair of arcuate grooves and traversed by a low median septum. The cardinal process is composed of numerous thin lamellae arranged approximately parallel to the plane of symmetry.

From 10 to 23 radially arranged plications have been observed on either side of the sinus. Bifurcation of these lateral plications is unknown. The fold and sinus bear from 2 to 6 plications. The occurrence of plications between the bounding plications and the primary plications is rare. In no case has bifurcation of the sinal plications been observed. Both plications and interspaces are covered with fine longitudinal striations. These become particularly prominent along the mid-line of the sinus, probably due to the better preservation of this area. The interspaces are broader than the plications. Sinal plications are finer than the lateral plications.

The species name refers to the strikingly wide variation of shell form encountered in this species.

Occurrence.—All types are from locality 200* in the Gneudna Limestone, 3.5 miles south of Gneudna Well, Williambury Station, North-West Basin, Western Australia.

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*This and succeeding locality numbers refer to the field numbers of the Bureau of Mineral Resources.

Subfamily Cyrtospiriferinae Termier and Termier, 1949

Genus *Cyrtospirifer* Nalivkin, 1918

In 1918 Nalivkin established *Cyrtospirifer* as a new subgenus of *Spirifer*, with *Spirifer verneuili* Murchison as type species. Many recent authors have accorded full generic rank to the group of *Spirifer verneuili*. There can be no doubt that this practice is justified, since fundamental morphological differences occur between the group of *Spirifer striatus*, the type species of *Spirifer*, and the group of *Spirifer verneuili*. The dental lamellae of *Cyrtospirifer* are primitive in that they extend anteriorly along the floor of the pedicle valve for a considerable distance. The two dental lamellae are also joined at about their mid-height by a well developed subdelthyrial platform. The dental lamellae of *Spirifer* s.s. are confined to the rostral area, and a delthyrial platform is never well developed. Substantial differences in the form of the descending lamellae and development of the jugal process also appear to exist between the two genera, but insufficient information is at present available for them to be stated with any degree of certainty. Obvious differences occur in the macro-ornamentation. *Cyrtospirifer* has numerous fine plications. They are simple on the flanks, but complexly bifurcated and intercalated in the fold and sinus. *Spirifer* s.s. has fewer plications on both the flanks and the sinus. They are usually simple on the flanks, but in the lower Pennsylvanian strong fasciculate costae begin to develop. This evolutionary trend culminates in the Pennsylvanian and Permian genus *Neospirifer*, a form with weakly developed dental lamellae and strongly fasciculate ribs on the flanks. *Spirifer* and *Cyrtospirifer* are also separated stratigraphically. *Cyrtospirifer* is known only from the Frasnian, while *Spirifer* s.s. is probably confined to the Mississippian and lower Pennsylvanian, although there are doubtful reports of its occurrence in the Upper Devonian. *Neospirifer* first appears at the base of the Pennsylvanian and continues throughout the Permian.

Since Nalivkin established *Cyrtospirifer*, there have been many attempts to set up other subgenera of *Spirifer*. The object of this practice has in many cases been to emphasise the presence of large morphological series which are not sufficiently different from other geographically isolated faunules to warrant generic status. Considering the extreme variability characteristic of the Upper Palaeozoic Spiriferidae, it becomes evident that these groups are of dubious value. The creation of subgenera is not common practice amongst students of Palaeozoic brachiopods. Subsequent authors have thus tended to give full generic status to these groups, without critically examining the morphological criteria on which they are differentiated. The new genera and subgenera of spiriferids proposed

by Grabau (1931) and Tien (1938) will be considered, since many of them obviously belong with the group of *Spirifer verneuili* in the genus *Cyrtospirifer*.

In 1931 Grabau proposed *Sinospirifer* as a subgenus of *Spirifer* for the group of *Spirifer sinensis*. He believed these brachiopods to constitute a morphological series whose development and differentiation occurred in the epeiric waters which covered southern China in Upper Devonian times. The Chinese forms were described as possessing "certain characteristics which stamp them as a morphological group (or *Formenreihe*) and enable one readily to distinguish them from most of the related European and American forms." However, the only character which Grabau mentions as being distinctive of the Chinese forms is their small size, although he goes into some detail to explain that the macroscopic ornamentation of the Chinese group is identical with that of the European forms. This fact assumes greater significance in the light of Grabau's statement that the mode and appearance of the sinal plications in the pedicle valve has "definite morphological value and may easily assume the first rank among the variable morphic structures." Many European forms referred to *Cyrtospirifer verneuili* are however, no larger than the average Chinese form, while the Russian forms do not in general appear to be any larger than those found in China. Thus although the *Cyrtospirifer sinensis* group may represent a morphological series, it is almost identical with the groups of *Cyrtospirifer* common in the Upper Devonian of America, Europe, North Africa and Australia. *Sinospirifer* Grabau should then be considered as a subjective synonym of the genus *Cyrtospirifer* Nalivkin, since the accordance of subgeneric status to geographical groups can only produce confused taxonomy.

In 1934 Grabau restricted the subgenus *Sinospirifer* to those forms with two primary sinal plications. The group previously included in *Sinospirifer* but possessing a single symmetrically placed primary sinal plication was separated out as a new sub-genus of *Spirifer*, namely *Centrospirifer*, with *Spirifer chaoi* Grabau as genotype. Substantial variations in the nature of the sinal plications (figs. 1 and 3) are noticeable on many specimens, between one side of the sinus and the other. Intra-specific variation is considerable, and inter-specific variation is pronounced. *Centrospirifer* Grabau is thus to be considered as a subjective synonym of *Cyrtospirifer*, since it was founded on morphological features of no more than specific value.

Tien (1938) further subdivided *Sinospirifer* (*emend* Grabau 1934), separating out two new subgenera of *Spirifer. Tenticospirifer*, with *Spirifer tenticulum* Vernueil as type species, included forms similar to *Sinospirifer* in most respects, but having a hemipyramidal pedicle valve. Other supposedly characteristic features were the thin shell, thin socket plates, absence of calcareous filling matter in the rostral area, and absence of a median septum on the floor of the brachial valve. All gradations of shell convexity from equi-biconvex to almost plano-pyramidal may be traced in the Chinese group of *Spirifer sinensis*. From the point of view of shell shape the group of *Spirifer tenticulum* then appears to represent extreme forms in a more or less continuous (normal) variation. The other features mentioned as distinctive are largely a function of age, and are certainly of no greater than specific value. The cellulose pull technique used in the present investigation showed the growth lamellae clearly. Cross-sections through the rostral area of the Western Australian specimens showed the contour of the internal surface of the valves to change during ontogeny. Fine morphological features such as the rostral cavity and the dorsal and ventral septa were generally obliterated in the gerontic growth stage by deposition of a thick layer of calcite in the vicinity of the rostral area. *Tenticospirifer* Tien is thus to be considered as a subjective synonym of *Cyrtospirifer*. *Hunanospirifer* (Tien 1938) was proposed as a new subgenus of *Spirifer* with *Spirifer wangi* as type species. *Hunanospirifer* was stated to differ from *Sinospirifer* and *Tenticospirifer* "principally in the feature of the hinge plate which is at first a solid one, being sharply arched above and perfectly flat below, but a little further down, the lower surface of the plate becomes divided in the centre by a small semi-circle." The only interpretation which can be applied to this is that the hinge plate thins between the sockets. This occurs almost universally amongst the spiriferids and can not constitute a valid basis for the creation of a new subgenus. *Hunanospirifer* Tien is thus to be considered as a subjective synonym of *Cyrtospirifer*.

Schizospirifer was proposed by Grabau in 1931 as a new subgenus of *Spirifer*, with *Spirifer latistriatus* Frech as type species. Grabau (1931, p. 354) states that Frech's description of *Spirifer latistriatus* is "worthless" but goes on to found *Schizospirifer* on Frech's work together with observations on one poorly preserved specimen in his own collections. Insufficient is known of this Middle Devonian species to correlate it with any existing genus. The presence of coarse bifurcating lateral plications seems to prohibit *Spirifer latistriatus* from being considered as a primitive *Cyrtospirifer*. Further investigation is needed before the subgeneric group of *Spirifer latistriatus* becomes recognisable and can be assigned to some generic group.

Platyspirifer was proposed by Grabau in 1931 for spiriferids similar to the group of *Cyrtospirifer sinensis* but having a hinge line slightly shorter than the maximum width of the shell. He selected *Schizophoria paronai* Martelli as the genotype. The species at present assigned to *Cyrtospirifer* are characterized by extreme variation of both the ratio of length to breadth and the position of greatest width of the shell. Shell ratios also vary markedly during the ontogeny of the individual. With these facts in mind, it is doubtful whether the specimens Grabau groups to constitute *Platyspirifer* even belong to valid species. There can be no doubt that *Platyspirifer* Grabau should be suppressed as a subjective synonym of *Cyrtospirifer*.

Spirifer padaukpinensis Reed, from the Padaukpin Limestone of the Northern Shan States of Burma, was used by Grabau (1931) as the type species of *Indospirifer,* a new subgenus of *Spirifer.* This rather distinct group is known only from the Middle Devonian of Asia. It is not closely related to *Cyrtospirifer.* The ribs of *Indospirifer* are far less numerous than those of *Cyrtospirifer.* They bear numerous fine striae which begin in the grooves and diverge fanwise onto the ribs, where they disappear. The internal structures are unknown, but it is probable that future study will prove this group worthy of generic status.

A further middle Devonian group was segregated by Grabau (1931) under the new genus *Plectospirifer,* with *Spirifer (Plectospirifer) peimi* Grabau as type species. The flanks bear coarse ribs, either simple or exhibiting bifurcation. The sinus may be smooth or characterized by finer sinal plications. In the latter case there is usually a single median primary plication. The shell surface is characterized by regular growth lamellae bearing radial striations; this prompted Grabau to place *Plectospirifer* amongst the Reticulariinae of Waagen. Unlike many of the Spiriferidae, *Plectospirifer* has its delthyrium closed in the manner usual amongst Beecher's old group, the Telotremata. The delthyrium is partially closed by a deltidium originating as a pair of discrete plates on either flank of the delthyrium. In many cases shell material is resorbed, so that the pedicle foramen occupies the position of the beak on the pedicle valve. Strong dental lamellae are present, but detailed internal structures are not well known. This group probably represents a valid genus.

Cyrtiopsis was proposed as a new genus by Grabau (1933) with *Cyrtiopsis davidsoni* Grabau as type species. He drew attention to the similarity between *Cyrtiopsis* and the "Upper Devonian Spirifers" and came to the conclusion that *Cyrtiopsis* differed from them "only in the persistence of the pseudodeltidium which moreover is pierced".

In most species of *Cyrtospirifer,* the plates which close the delthyrial openings are unknown. Two narrow grooves, however, invariably appear on the edge of the palintrope, and it seems reasonable to assume that their function was to lodge the plate or plates which closed the delthyrium. Many species of *Cyrtospirifer* have a large delthyrial opening, and it is unlikely that these forms would have survived without some efficent method of sealing that part of the delthyrial cavity not occupied by the pedicle. Closely related forms to those in which this apparatus for closing the delthyrium is not preserved, do in fact, possess a pseudodeltidium *(Cyrtospirifer verneuili* and *Cyrtospirifer brevicardinis).* It thus seems probable that the absence in the fossil state of apparatus for closing the delthyrium does not constitute proof that this apparatus did not exist. It appears that the pedicle had atrophied in many of the middle and late Palaeozoic spiriferids and the pseudodeltidia or deltidia

were loosely attached to the palintrope, and consequently lost during fossilisation. A poorly preserved specimen in the writer's collections from Chimay (Belgium) has been identified as *Cyrtospirifer verneuili.* This specimen shows a triangular, convex pseudodeltidium, but does not show a pedicle perforation. This absence of a pedicle foramen is readily explained in terms of the degeneration of the pedicle. In view of the evidence presented, it does not appear reasonable to maintain *Cyrtiopsis* as a valid genus merely on its possession of a perforate pseudodeltidium.

Substantial differences between the two genera do, however, occur. The long convergent curved dental lamellae of *Cyrtiopsis* differ from the shorter divergent lamellae of *Cyrtospirifer.* *Cyrtiopsis* is also generally more brachythyrid and has a delicate but distinct micro-ornamentation consisting of radial striations. Crickmay has also shown that at least in North America the genus *Cyrtospirifer* is restricted to Frasnian equivalents, while *Cyrtiopsis* is restricted to Famennian equivalents. *Cyrtiopsis* must thus remain as a valid genus, but for different reasons to those advanced by the original author.

That *Theodossia* Nalivkin lies close to *Cyrtospirifer* was revealed by a study of the literature, and confirmed by the examination of specimens of *Theodossia hungerfordii* Hall from the Hackberry formation of Iowa. However, the two genera differ slightly in both macro-ornamentation and the shape of the fold and sinus. Despite the great variation in the shape and placement of the plications in *Cyrtospirifer,* there is a common basic design which is maintained throughout the genus. The bounding plications are the most pronounced and the lateral plications become finer towards the cardinal extremities. Plications are usually appreciably finer in the sinus, where they range in size according to their order of appearance. The sinus is not always well developed, but the bounding plications may be readily detected and the sinus can always be traced to the beak. The plications of *Theodossia* are finer than those of *Cyrtospirifer.* They increase in thickness from the cardinal extremities towards the sinus. It is always difficult and generally impossible to exactly delimit the boundary of the sinus of *Theodossia,* since the bounding plications do not differ appreciably from the plications of the flanks or the sinus. The sinus is shallow and is not developed until the animal has almost reached maturity. It is thus observed only in the anterior part of most shells, where it appears as a gentle undulation which gradually merges into the flanks. The nature of the sinus must have been related to the intensity of respiratory exchanges of the organism. Significant differences in the sinus of *Cyrtospirifer* and *Theodossia* have been demonstrated, and it is the opinion of the present author that these differences, together with the dissimilarity of the plications, warrant the retention of the two groups as separate genera.

TABLE IV

Measurements (in mm.) of Cyrtospirifer minilyaensis *Glenister, n.sp.*

Growth stage	Neanic		Ephebic		Gerontic
Catalogue number	457	458	459	460	477*
Plate	3—14-18	3—19-23	3—24-27	3—28-32	3—9-13
Figures	3—1	3—2	3—3	3—4	3—5
Height of pedicle valve	13·2	13·9	20·2	20·0	21·2
Length on curvature (centre)	14·3	15·7	23·0	24·5	25·1
Height of brachial valve	12·9	13·4	18·7	19·5	18·6
Length on curvature (centre)	15·5	15·7	25·0	24·0	22·9
Width along hinge line	24·0	23·0	25·7	27·0	25·4
Maximum width of shell	24·0	23·0	25·7	27·5	25·4
Maximum height of palintrope	4·9	4·6	5·2	6·0	7·3
Thickness of shell	8·8	9·2	14·5	15·6	13·9
Maximum width of sinus (anterior)	5·4	6·9	11·6	9·4	10·8
Number of lateral plications	30	26	28	30	28
Shell index of pedicle valve	1·70	1·47	1·12	1·10	1·01
Shell index of brachial valve	1·55	1·47	1·03	1·12	1·11

* Holotype

TABLE V

Shell indices for the pedicle valve of Cyrtospirifer minilyaensis *Glenister, n.sp., measured on growth lines. Measurements in mm.*

Catalogue number	477*						
Growth stage	Nepionic		Neanic		Ephebic		Gerontic
Length on curvature (centre)	6·0	9·1	14·0	15·4	19·8	23·2	25·1
Corresponding width along hinge line	10·9	16·2	22·4	22·8	25·2	25·3	25·4
Shell index	1·81	1·78	1·60	1·48	1·27	1·09	1·01

* Holotype.

Cyrtospirifer minilyaensis Glenister, n.sp.

Plate 3—9-32; figs. 3—1-5, 5—1-21; tables IV and V

Description.—The holotype, 2 paratypes, 4 hypotypes, and 95 other specimens belonging to this species were available to the author. The shells are inequally biconvex, the pedicle valve being deep and hemi-pyramidal and the brachial valve shallowly convex. Immature shells are much wider than long and have acutely angular cardinal extremities. Mature specimens are slightly wider than long, but are sub-quadrate with broadly rounded anterior-lateral margins and cardinal angles measuring slightly less than a right angle. The gerontic growth stage is marked by the development of small ears and the approach to unity of the shell index of the pedicle valve. In exceptional cases the greatest width may no longer lie along the hinge line. The anterior commissure is broadly uniplicate.

The pedicle valve is strongly arched laterally but only weakly convex along the plane of symmetry. The sinus is broad and shallowly rounded, extending from the point of the beak to the anterior margin, where it continues as a shallow rounded projection. The palintrope is high, triangular, either flat or weakly concave, and apsacline in all growth stages. Growth lines parallel to the hinge line are frequently preserved, and a few well-preserved specimens show the area to be finely striated at right angles to the growth lines. A broad triangular delthyrium, having its apex immediately below the beak, bisects the palintrope. Apparatus for closing the delythyrium is not preserved in any of the specimens in the author's collections.

The brachial valve is flatly convex with shallowly concave posterior-lateral margins. The umbo is weakly developed and partially overhangs a low cardinal area which is bisected by a broad notothyrium and is generally orthocline. A weakly convex fold extends from the beak to the anterior margin, where it is truncated by the sinal extension of the pedicle valve.

The dental lamellae are thin and diverge anteriorly along the floor of the pedicle valve for slightly more than a third of the distance to the anterior margin of the conch. They support two strong teeth. The area of muscle attachment is crossed by fine radially-directed striations and bears a median fold at the posterior end. Lines of growth in the dental lamellae show that they are composed of two distinct elements. The growth lines of the outer layer